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Effect of water stress on seedling growth of four tropical dry deciduous tree species under an elevated CO_2 regime

Due to fossil-fuel burning and deforestation, the concentration of atmospheric CO_2 may exceed 700 ppm by the end of the present century[1]. The elevated CO_2 affects plants either by increasing carbon fixation due to repression of photorespiration and increased substrate supply, or by decreased water loss due to partial closure of the stomata or by CO_2-driven changes in ecosystem nutrient dynamics and changed soil structure[2]. Dry tropical forests often experience frequent droughts during which an increased soil-water deficit develops[3] and seedlings experience desiccation[4]. The present study investigates the interactive impact of water stress and elevated CO_2 on seedlings of four native tree species, *Acacia catechu* Willd., *Bauhinia variegata* L., *Dalbergia latifolia* Roxb. and *Tectona grandis* L.f. We address two broad questions: (a) Do elevated CO_2 and water stress affect seedling growth differentially in different species? (b) Does the elevated CO_2 interact with water stress in affecting the growth performance of seedlings?

The interactive impact of two levels of CO_2 concentration and four water levels was assessed in a pot culture experiment conducted at the Botanical Garden, Department of Botany, Banaras Hindu University, Varanasi, India (25°18′N, 83°03′E, 129 m asl). One-week-old seedlings of each species were transplanted into earthen pots (1710 cubic cm), one seedling per pot. The soil in the pots was inceptisol (33% sand, 16% clay and 33% water holding capacity (WHC)). Organic C, total N and total P were 2.4, 0.18 and 0.03% respectively. The transplanted seedlings were equally well-watered during the first three weeks. Seedlings were subsequently subjected to four soil moisture levels: 1, ½, ⅓ and ¼ WHC following Khurana and Singh[5,6].

For exposing seedlings to a relatively elevated CO_2 level, the method described by Khurana and Singh[7] and Devakumar *et al.*[8] was followed, in which higher concentration of CO_2 (700–750 ppm) was obtained from decomposition of organic matter. A set of 24 (4 water levels × 3 replicates × 2 sampling dates = 24) pots was used for each species in ambient and elevated CO_2.

Before exposure of these seedlings to elevated CO_2, a set of three seedlings was harvested to record the initial growth parameters (0-day harvest). After 30 days of exposure, three seedlings of each species from each treatment were harvested. Height and leaf area were recorded. Leaf area per plant was obtained as the product of number and area of leaves. Leaf area for each plant species was calculated from regression equations relating leaf area to leaf biomass, developed from destructive harvests of leaves from a separate set of seedlings. Plants were then separated into stem, leaves and roots. All plant parts were oven-dried at 80°C to constant weight. Similarly, after 60 days of exposure, the remaining plants were harvested and final growth data were recorded.

The impact of species, water level, CO_2 concentration and days of exposure was analysed through multivariate ANOVA.

Results of the present study show that growth performance of seedlings significantly differed across species, water stress and CO_2 level. Interactions species × water level, species × CO_2 level and water level × CO_2 level were significant. Water stress had a profound adverse effect on the growth performance of seedlings of all the four tree species. Seedlings of *A. catechu* did not survive at ¼ WHC beyond 30 days and those of *B. variegata* did not

Table 1. Effect of water stress on selected growth traits of seedlings of four species of tropical dry deciduous trees grown under four water and two CO_2 levels

		1 WHC		½ WHC		⅓ WHC		¼ WHC	
Species	Days	A-CO_2	E-CO_2	A-CO_2	E-CO_2	A-CO_2	E-CO_2	A-CO_2	E-CO_2
Leaf area (sq. cm plant^{-1})									
Acacia catechu	30	489 ± 54.1	799 ± 38.3	260 ± 23.3	541 ± 21.3	158 ± 16.2	271 ± 26.8	61 ± 3.8	90 ± 5.3
	60	667 ± 57.6	1435 ± 79.0	544 ± 8.1	958 ± 133.8	327 ± 16.2	529 ± 33.8	0 ± 0.0	0 ± 0.0
Bauhinia variegata	30	232 ± 31.4	501 ± 17.1	105 ± 7.4	278 ± 17.2	63 ± 3.5	78 ± 3.3	0 ± 0.0	0 ± 0.0
	60	500 ± 20.5	845 ± 31.8	151 ± 7.4	593 ± 46.5	121 ± 3.3	340 ± 52.9	0 ± 0.0	0 ± 0.0
Dalbergia latifolia	30	77 ± 8.5	156 ± 19.4	49 ± 0.5	94 ± 4.2	42 ± 0.8	57 ± 3.7	19 ± 0.5	26 ± 1.4
	60	387 ± 14.2	617 ± 66.9	290 ± 20.0	402 ± 16.3	184 ± 10.0	204 ± 10.0	30 ± 0.2	36 ± 1.4
Tectona grandis	30	127 ± 5.5	183 ± 6.5	85 ± 6.7	153 ± 5.3	39 ± 3.6	80 ± 2.1	17 ± 0.5	26 ± 0.6
	60	331 ± 36.3	337 ± 37.5	218 ± 35.1	245 ± 19.5	120 ± 6.5	180 ± 13.6	55 ± 2.5	76 ± 6.7
Leaf biomass (g plant^{-1})									
A. catechu	30	0.3 ± 0.0	0.4 ± 0.0	0.1 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	60	0.4 ± 0.0	0.8 ± 0.0	0.3 ± 0.1	0.5 ± 0.1	0.2 ± 0.0	0.3 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
B. variegata	30	1.0 ± 0.1	2.2 ± 0.1	0.5 ± 0.1	1.2 ± 0.1	0.3 ± 0.0	0.4 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	60	2.2 ± 0.1	3.7 ± 0.1	0.7 ± 0.0	2.6 ± 0.2	0.5 ± 0.0	1.5 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
D. latifolia	30	0.2 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.12 ± 0.0	0.0 ± 0.0	0.1 ± 0.0
	60	0.8 ± 0.0	1.3 ± 0.0	0.6 ± 0.0	0.8 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
T. grandis	30	0.7 ± 0.1	1.1 ± 0.0	0.5 ± 0.0	0.9 ± 0.0	0.2 ± 0.0	0.5 ± 0.0	0.1 ± 0.0	0.2 ± 0.0
	60	1.9 ± 0.2	2.2 ± 0.2	1.1 ± 0.2	1.4 ± 0.1	0.7 ± 0.0	1.0 ± 0.1	0.3 ± 0.0	0.4 ± 0.0
Plant biomass (g plant^{-1})									
A. catechu	30	0.5 ± 0.0	0.8 ± 0.0	0.4 ± 0.0	0.6 ± 0.0	0.3 ± 0.0	0.5 ± 0.0	0.2 ± 0.0	0.5 ± 0.0
	60	0.8 ± 0.1	1.7 ± 0.1	1.2 ± 0.1	1.8 ± 0.1	1.2 ± 0.2	2.4 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
B. variegata	30	1.5 ± 0.2	3 ± 0.1	0.8 ± 0.0	1.9 ± 0.1	0.5 ± 0.0	0.8 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	60	4.6 ± 0.2	8.1 ± 0.4	2.7 ± 0.0	6.1 ± 0.3	2.6 ± 0.0	4.7 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
D. latifolia	30	0.5 ± 0.0	1 ± 0.1	0.4 ± 0.0	0.7 ± 0.0	0.3 ± 0.0	0.5 ± 0.0	0.3 ± 0	0.4 ± 0.0
	60	1.5 ± 0.1	2.3 ± 0.2	1.3 ± 0.1	1.8 ± 0.0	1 ± 0.1	1.3 ± 0.0	0.7 ± 0.1	0.9 ± 0.0
T. grandis	30	1.2 ± 0.0	1.8 ± 0.0	0.9 ± 0.0	1.5 ± 0.0	0.6 ± 0.0	1.1 ± 0.1	0.4 ± 0.0	0.7 ± 0
	60	2.2 ± 0.5	3.5 ± 0.2	2.0 ± 0.2	2.8 ± 0.2	1.5 ± 0.5	2.7 ± 0.2	1.1 ± 0.0	2.0 ± 0.1

A-CO_2, Ambient CO_2; E-CO_2, Elevated CO_2.

survive at this moisture level for more than a week. The growth of seedlings of all the four species was better under elevated CO_2 regime at all soil-water levels.

At the end of 30 days, the seedlings of *A. catechu*, *D. latifolia* and *T. grandis* were only 36, 52 and 60% tall respectively, at ¼ WHC compared to those maintained at 1 WHC. At each water level, the seedlings were taller in high CO_2 environment compared to those at ambient CO_2 level. The magnitude of the positive effect of elevated CO_2 differed among species and the level of water stress. For example, while seedlings of *T. grandis* exposed to the two CO_2 levels showed maximum per cent difference in height at ⅓ WHC, those of *B. variegata* realized maximum increase at ½ WHC and seedlings of *A. catechu* and *D. latifolia* at 1 WHC.

Seedlings of *A. catechu*, *D. latifolia* and *T. grandis* had 86, 71 and 45% more leaves, 88, 81 and 86% more leaf biomass, and 81, 76 and 87% greater leaf area at 1 WHC respectively, than those at ¼ WHC at the end of 30 days (Table 1). At each soil-water level, the seedlings had more leaves, greater leaf biomass and greater leaf area in high CO_2 environment compared to those at ambient CO_2 level. However, the magnitude of positive effect of high CO_2 environment varied across species and water level. For example, the per cent difference in leaf area per plant between the two CO_2 levels was maximum at ½ WHC in *A. catechu*, *B. variegata* and *D. latifolia*, while in *T. grandis* the difference was highest at ⅓ WHC.

Seedlings of *A. catechu*, *D. latifolia* and *T. grandis* had 51, 48 and 64% higher biomass at 1 WHC respectively, than those maintained at ¼ WHC at the end of 30 days (Table 1). Lowest plant biomass in all the four species was observed under ¼ moisture stress condition at ambient CO_2 and maximum under 1 WHC under elevated CO_2. Enhancement in biomass due to exposure to high CO_2 environment at different stress levels also varied across species. Biomass partitioning, expressed as root/shoot (*R*/*S*) ratio, generally increased with an increase in water stress (Figure 1). This increase in *R*/*S* ratio was more pronounced under ambient CO_2, except for *D. latifolia* at 60 days and *T. grandis* at 30 days.

The effect of the period of exposure to elevated CO_2 was significant, and all growth traits exhibited smaller differences between the two CO_2 levels at 60 days compared to 30 days.

In our study, water stress significantly reduced the overall growth of seedlings of all the species, although the magnitude of the effect differed across species. Reduced seedling growth due to water stress has been reported for several other species[6,9].

Decreased leaf area in response to water stress in this study was due to reduction in total number of leaves as well as poor expansion of leaves in stressed environment, indicating an adaptation to avoid water loss through transpiration. Khurana and Singh[6] have reported 29–93% decrease in leaf area of *Albizia procera*, *Acacia nilotica*, *Phyllanthus emblica*, *Terminalia arjuna* and *T. chebula*. Reduction in leaf area with increasing water stress demonstrates the ability of a species to tolerate and acclimate to a broad range of water levels by morphogenic plastic responses[6,10].

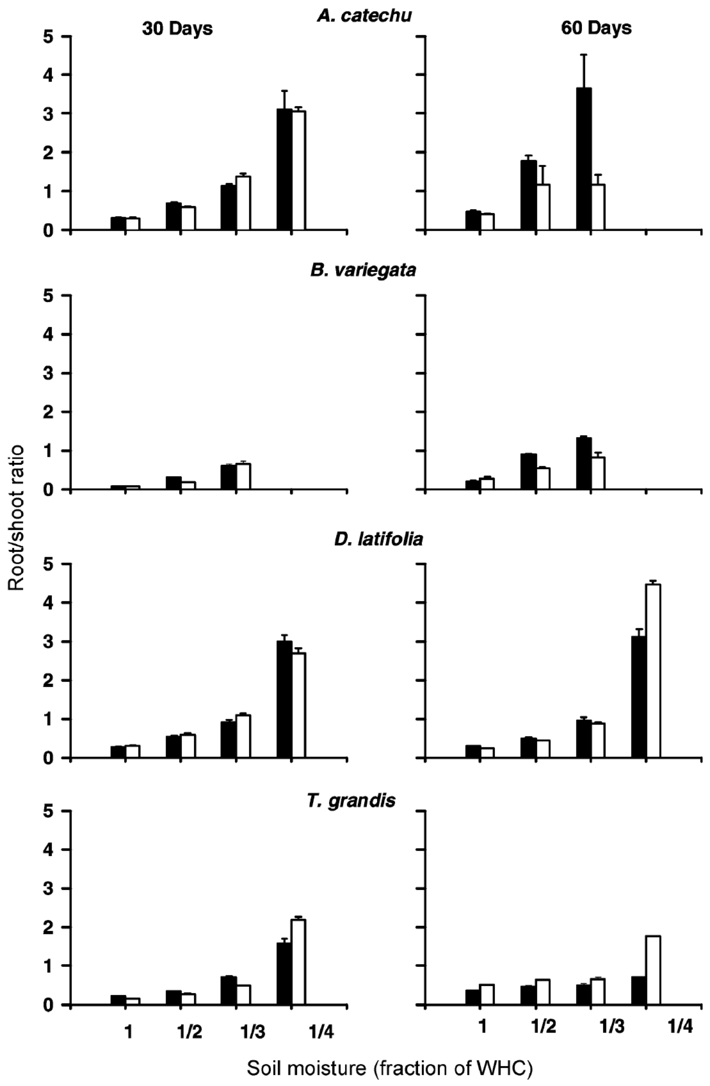

Figure 1. Root/shoot ratio of seedlings grown at four soil-water and two CO_2 levels (shaded bars represent ambient CO_2 and unshaded bars represent elevated CO_2).

Exposure to elevated CO_2 resulted in 60% enhancement in the biomass of temperate deciduous tree species[11] and 100–300% increase in biomass of dry deciduous tree seedlings[7]. These values correspond with the increase in biomass of 40–136% in this study at different water stress levels under elevated CO_2 regime.

There was a consistent shift in resource allocation from shoot to root at low moisture levels, as indicated by an increase in *R*/*S* ratio. Plants living in low-rainfall habitats might benefit from having a large root system, as they will compete better for water[12]. McConnaughay and Coleman[13] hypothesized that the higher *R*/*S* ratio of water-stressed plants was consistent with optimal foraging behaviour in which plants shifted the partitioning of carbohydrates to belowground foraging structure, even in the absence of a true allocation pattern.

However, after 60 days of exposure to CO_2, per cent enhancement in biomass and other growth traits was down-regulated. The major reasons for this could be: physical distortion of chloroplast due to accumulation of starch, inhibition of sucrose phosphate synthetase to enhance starch synthesis, competition of phosphorylated sugars for binding sites on Rubisco enzyme, increase in the activity of carbonic anhydrase and inability of the Calvin cycle to regenerate ribulose bisphosphate or orthophosphate[14,15]. There was no consistent shift in resource allocation from the shoot to root at high CO_2 levels, as indicated by an enhancement in root biomass and *R*/*S* ratio.

Although species indicated individualistic response to the CO_2 × water stress interaction, it can be inferred that increase in CO_2 might help in improving resistance to water stress, which is known to be a major cause of seedling mortality in the dry tropical forest of India[5].

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